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Article (Published Version)

Neuropsychologia 51 (2013) 2909–2917

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubber-hand illusion

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ARTICLE INFO

Article history:
Received 22 May 2013
Received in revised form
12 August 2013
Accepted 19 August 2013
Available online 28 August 2013

Keywords:
Interoception
Rubber hand illusion
Multisensory integration
Experience of body ownership
Augmented reality
Predictive coding

ABSTRACT

Identifying with a body is central to being a conscious self. The now classic "rubber hand illusion" demonstrates that the experience of body-ownership can be modulated by manipulating the timing of exteroceptive (visual and tactile) body-related feedback. Moreover, the strength of this modulation is related to individual differences in sensitivity to internal bodily signals (interoception). However the interaction of exteroceptive and interoceptive signals in determining the experience of body-ownership within an individual remains poorly understood. Here, we demonstrate that this depends on the online integration of exteroceptive and interoceptive signals by implementing an innovative "cardiac rubber hand illusion" that combined computer-generated augmented-reality with feedback of interoceptive (cardiac) information. We show that both subjective and objective measures of virtual-hand ownership are enhanced by cardio-visual feedback in-time with the actual heartbeat, as compared to asynchronous feedback. We further show that these measures correlate with individual differences in interoceptive sensitivity, and are also modulated by the integration of proprioceptive signals instantiated using real-time visual remapping of finger movements to the virtual hand. Our results demonstrate that interoceptive signals directly influence the experience of body ownership via multisensory integration, and they lend support to models of conscious selfhood based on interoceptive predictive coding.

1. Introduction

The experience of body ownership (EBO) – of owning and identifying with a particular body – is a central aspect of selfhood (Bermudez, Marcel, & Eilan, 1995; Blanke, 2012; Blanke & Metzinger, 2009). Although under normal circumstances EBO appears highly stable, there is increasing evidence to indicate that EBO depends on dynamic "on-the-fly" multisensory integration of self-related signals and is hence surprisingly open to change. In the "rubber hand illusion" (RHI), the stroking of an artificial hand synchronously with a participant's real hand, while visual attention is focused on the artificial hand, leads the participant to experience the artificial hand as part of his or her own body (Botvinick & Cohen, 1998). Similar synchronous visuo-tactile stimulation can enhance self-identification with the face of another (the "enfacement illusion", Sforza, Bufalari, Haggard, & Aglioti, 2010; Tsakiris, 2008) and can even facilitate an illusory sense of identification with a virtual whole body (Lenggenhager, Tadi, Metzinger, & Blanke, 2007) or with the body of another person (Petkova & Ehrsson, 2008). These studies exemplify the strong influence of exteroceptive inputs – the perception of the body *from the outside* – in shaping self-models based on multisensory integration. A separate tradition emphasizes the importance of *interoception* – the sense of the internal physiological state of the body – in underpinning the sense of self (Craig, 2009; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Damasio, 2010; Seth, Suzuki, & Critchley, 2011). Interoceptive representations reflect the perception of the body *from the inside* and contribute to the regulation of physiological integrity (homeostasis) and associated affective feelings, drives and emotions. A central theme within these models is that selfhood emerges through elaboration of interoceptive representations and their integration with exteroceptive signals within cortical regions, notably the anterior portions of the insular cortex.

Given these two traditions, it is natural to ask how exteroceptive and interoceptive signals interact in specifying EBO and the sense of self. Tsakiris and colleagues capitalized on individual variation in interoceptive sensitivity (IS), which refers to a person's ability to detect their own interoceptive signals. They report that participants with lower IS are more susceptible to the RHI (Tsakiris, Tajadura-Jimenez, & Costantini, 2011) and exhibit larger

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http://dx.doi.org/10.1016/j.neuropsychologia.2013.08.014

changes in self-other boundaries during the enfacement illusion (Tajadura-Jimenez, Longo, Coleman, & Tsakiris, 2012; Tajadura-Jimenez & Tsakiris, in press). IS is standardly gauged as the capacity to report accurately the timing of one's heartbeat at rest and is considered a stable characterological trait (Schandry, 1981). Other evidence links physiological state to EBO: Perceived threat or injury to an artificial hand during the RHI leads to increased skin conductance responses (Armel & Ramachandran, 2003). Induction of the RHI also leads to decreased temperature (Moseley et al., 2008) and increased histamine reactivity (Barnsley et al., 2011) of the real hand, while cooling the real hand increases susceptibility to the RHI (Kammers, Rose, & Haggard, 2011). Although these studies provide circumstantial support for the interaction of exteroceptive with interoceptive processes in EBO, they do not address the important question of how this interaction is supported by multisensory integration across these different domains.

Here, we address this question by implementing a novel “cardiac rubber hand illusion” capitalizing on augmented reality (AR) technology and integrating this with physiological (cardiac) monitoring. This approach allows us to superimpose a “virtual rubber hand” within a participant's visual field, the visual appearance of which can be modulated by cardiac signals such that the modulation is either in synchrony, or out of synchrony, with the participant's actual heartbeat. Feedback synchronicity thereby directly probes interactions between exteroceptive perception and short-term *interoceptive* representations of heartbeats. The usefulness of this approach has very recently been explored in the related context of the full-body illusion (Aspell et al., in press). Distinctively, our setup also enables an AR implementation of the RHI paradigm involving tactile-visual feedback, and – extending the classical RHI – proprioceptive-visual integration wherein movements of the real hand are dynamically mirrored by corresponding movements of the virtual hand. Our primary finding is that synchronous – as compared to asynchronous – cardio-visual feedback leads to an enhanced experience of ownership of the virtual hand, indicating that EBO in this context can be modulated by multisensory integration across exteroceptive and interoceptive domains. We also show that accurate visual feedback of intentional hand movements, supporting peri-hand visual-proprioceptive coherence provides a powerful cue for EBO that can overshadow cardio-visual feedback. Lastly, we examined how the magnitude of our results reflected individual differences in IS, testing the prediction that heightened IS will attenuate EBO (Tsakiris et al., 2011) yet exaggerate interaction between exteroceptive and interoceptive manipulations. We interpret our results in the light of emerging models of selfhood based on “predictive processing” which focus existing multisensory integration accounts (e.g., Makin, Holmes, & Ehrsson, 2008) by positing that experiences of selfhood and body ownership are determined by the brain's estimation of the most likely interpretation of the ensemble of self-related signals, computed according to Bayesian principles (Apps & Tsakiris, 2013; Friston, Daunizeau, Kilner, & Kiebel, 2010; Seth et al., 2011).

2. Materials and methods

2.1. Participants

Twenty-one volunteers took part in the experiment (mean age 21.2; SE=3.1; 10 male; two left handed). Participants were recruited via our laboratory website and notice boards. The study was approved by the ethics committee of the School of

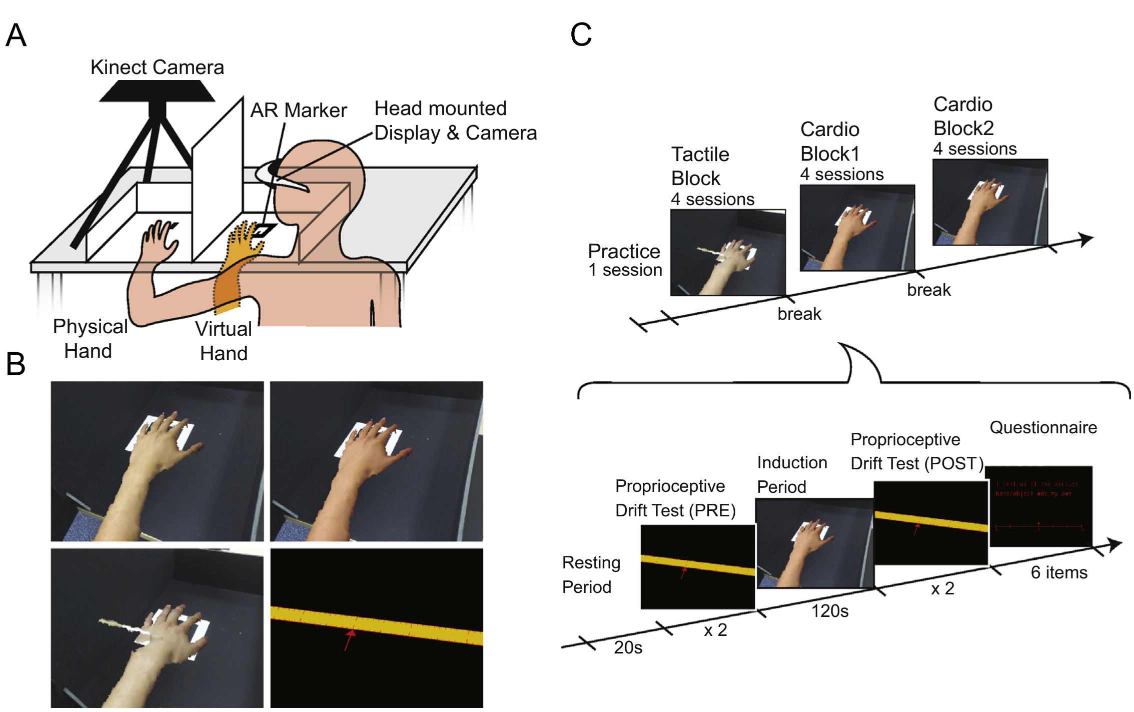

Fig. 1. Experimental setup and design. (A) Participants sat facing a desk so that their physical hand was out of sight when they looked downward and ahead. A 3D model of the real hand was captured by the Kinect and used to generate a real-time virtual hand which was projected into the head-mounted display (HMD) at the location of the AR marker. Subjects wore a front-facing camera connected to the HMD so they saw the camera image superimposed with the virtual hand. They also wore a pulse-oximeter to measure heartbeat timings, and they used their right hand to make behavioral responses. (B) Cardio-visual feedback was implemented by changing the color of the virtual hand from its natural color (top-left) towards red (top-right) and back, over 500 ms either synchronously or asynchronously with the heartbeat. Tactile feedback was given by a paintbrush, which was rendered into the AR environment (bottom-left). Objective measurements of virtual hand ownership depended on a, proprioceptive drift' (PD) test adapted for the AR environment, involving a virtual measure and cursor whose scale and position were aligned with the real world (bottom-right). (C) The main experiment consisted of three blocks of four trials each, preceded by a practice trial. Each trial consisted of two PD tests flanking an induction period during which either cardio-visual or tactile-visual feedback was provided (120 s). Each trial ended with a questionnaire presented in the HMD. Before the main experiment each participant's interoceptive sensitivity was measured.

Psychology at the University of Sussex. All participants gave their informed consent prior to starting the experiment.

2.2. Experimental setup

Participants sat facing a desk with their left hand placed to the left of a vertical partition, out of sight (Fig. 1A). This hand was aligned with a small marker to ensure a distance between the real hand and virtual hand of 19 cm. Their body centre was situated to the right of the partition approximately 40 cm to the right of their real hand. They wore a head-mounted-display (HMD, HMZ-T2, Sony, Tokyo, Japan) fitted with a forward-facing camera (HD Pro Webcam C920, Logitech, Lausanne, Switzerland). The image presented in the HMD consisted of the real-time camera input superimposed with a three-dimensional real-time model of their real hand, which appeared spatially located to the right of the partition in an anatomically plausible position. Participants directed their gaze and attention on this location during the experiment. They used their right hand (also located outside the field of view) to make responses via a dedicated input device (PowerMate, Griffin Technology, TN, USA). During the main experiment they wore a pulse oximeter (XPOD with 8000AA finger clip sensory, Nonin Medical Inc., MN, USA) on their right index finger to obtain real-time cardiovascular timing information. This allowed us to modulate the visual appearance of the virtual hand as a function of cardiac cycle, thus implementing "cardio-visual feedback". In some conditions, the participant's left hand was gently stroked by the experimenter using a paintbrush at a frequency of $\sim$1 Hz (following the standard RHI paradigm), and the visual image of this stroking was also modeled and re-presented in the HMD to provide tactile-visual feedback. A video illustrating the setup and the experimental conditions is provided in Supplementary information.

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.neuropsychologia.2013.08.014.

2.3. Augmented reality and tactile/cardio-visual feedback

As shown in Fig. 1A, a Microsoft Kinect (Kinect for Windows, Microsoft, WA, US) was mounted above the table, facing downwards, 70 cm above the participant's real hand. We developed custom-software using the freely available "ARToolkit" (http://www.hitl.washington.edu/artoolkit/) to link the Kinect with the HMD and the head-mounted camera. Using this software, a 3D hand model captured by the Kinect was projected onto the location of a marker (AR marker) through the HMD, in real-time, so that the virtual hand appeared as part of the real world as seen through the HMD via the CMOS camera. Specifically, "point cloud" data (RGB images with accompanying depth maps) were streamed from the Kinect, trimmed by the 70 cm cut-off distance, and then directly rendered into the AR environment using OpenGL. In contrast to the classical RHI setup, our 3D hand model is highly photo-realistic and is capable of capturing and re-projecting hand-movements in real-time. In conditions requiring tactile-visual feedback, the paintbrush-stroking was also rendered into the AR environment, either synchronously or asynchronously (delayed by 500 ms) with the real paintbrush movements.

Cardio-visual feedback was implemented by using information from the pulse-oximeter to modify the real-time rendering of the 3D hand model (Fig. 1B). To compensate delay in oximeter data acquisition and processing we designed custom software which estimated the timing of each heartbeat based on the average period of the 10 preceding heartbeats (see below). Within the AR system, this was used to trigger a gentle pulsing of the color of the virtual hand to red, and back again. Each pulse lasted 500 ms during which the red component in the image linearly increased (250 ms) and then linearly diminished (250 ms). The peak redness was 40% of the maximum possible. During synchronous feedback, we delivered peak redness to coincide with the ejection of blood from the heart (systole). This required compensation for the temporal lag of the pulse oximeter and necessitated an estimation of cardiac cycle timing from previous heartbeats. Asynchronous feedback was implemented by changing the frequency of estimated heart-rate to be either slower (70%) or faster (130%). Slow and fast asynchronous trials occurred equally often for each participant and their timing was counterbalanced across participants.

Following our previously established procedures (Garfinkel et al., 2013; Gray et al., 2012; Gray, Minati, Paoletti, & Critchley, 2010) we estimated the cardiac R-wave (indicating ventricular depolarization) as occurring 350 ms preceding the peak of the finger pulse oximetry waveform, reflecting pulse transit time and the delay between R-wave and peak cardiac ejection. By considering (10) previous peaks we could predict the occurrence of each subsequent R-wave with validated accuracy ($<$20 ms s.d.). The peak color modulation in cardio-visual feedback was then timed to coincide with peak systolic pressure (200–250 ms, we used a value of 210 ms following estimated R-wave). This peak pressure is when aortic baroreceptors are most active and is also when heartbeats are typically perceived in tests of interoceptive sensitivity (Brener, Liu, & Ring, 1993; Wiens & Palmer, 2001). We note that time window for cardio-visual feedback has sufficient overlap with the period of peak systolic pressure to accommodate fluctuations due to signal processing and rendering ($\pm$70 ms) and any individual variation in pulse transit time (e.g., due to differences in arm length) of 100 ms or less (a range highly unlikely to be exceeded in our healthy young population). We further emphasize that the asynchronous feedback was truly asynchronous and distinct from minor phase shifts in the timing of visual feedback for any one individual.

2.4. Experimental procedure

Following a test of individual interoceptive sensitivity (see Section 2.7 below), each participant began the main experiment which was organized into three blocks, with each block containing four trials (Fig. 1C). Each trial started with a 20 s resting period in which only the background was shown through the HMD (i.e., no virtual hand). Following this was a first "proprioceptive drift" test, designed to measure ownership of the virtual hand objectively (see Section 2.5 below). After this came the "induction period" (120 s) during which the participant paid attention to their virtual hand; the nature of this period varied according to experimental condition (see below). After this came a second proprioceptive drift test, followed by a short questionnaire presented through the HMD, providing a subjective assessment of ownership (see Section 2.6, below). Each trial lasted $\sim$3.5 min and the entire experiment lasted $\sim$1.5 h. After each block participants took a short break during which they removed the HMD for comfort. Before the first block, a practice trial was provided to ensure that participants were familiar with the paradigm.

Induction periods in each trial were drawn from 1 of 3 different conditions, with each condition divided into synchronous and asynchronous feedback sub-conditions. In the first condition ("cardiac still") participants were instructed to keep their left hand still, and to focus their gaze and attention on the visual pulsing of the virtual hand. In the second condition ("cardiac move") participants were instructed to move their fingers without any constraints other than to keep their hand in the same place, while still focusing on the virtual hand. In both these conditions the virtual hand was modulated by cardio-visual feedback for the full 120 s. In the third condition ("tactile") the real hand was stroked with a paintbrush while tactile-visual feedback was presented via the HMD; again participants were asked to focus on the virtual hand. At the start of each trial, participants were informed of the corresponding condition ("cardiac still", "cardiac move", "tactile"); they were not informed whether the feedback would be synchronous or asynchronous. The first block contained only "tactile" trials. The second and third blocks contained both "cardiac still" and "cardiac move" trials, with trial order and feedback synchrony counterbalanced across participants.

2.5. Proprioceptive drift

Before and after each induction period participants were asked to indicate the perceived location of their real hand, providing a measure of proprioceptive drift (PD, Fig. 1). In each PD test, participants were presented via the HMD with a scene containing a virtual ruler, a cursor, and the AR marker. The remainder of the image was uniformly black. They were asked to use the input device to move the cursor to point to the perceived location of their left hand. PD was calculated as the distance (in cm) from the real hand to the perceived location. The position of the cursor and ruler relative to the AR marker position was randomly chosen in each test (in the range [$-$3, 0] cm from the actual left index finger position), preventing participants

Table 1
Subjective questionnaire. Q1 and Q3 assess subjectively the EBO of the virtual hand, while Q2 and Q4 are control questions which are designed to impose equivalent attentional demands without relating specifically to EBO. Q5 assesses whether subjects can detect synchronous as compared to asynchronous feedback. Responses were collected on a 7-point continuous visual analog scale with $-$3 representing "strongly disagree" and +3 "strongly agree", though any intermediate point could be selected.

Question	
Q1	It felt as if the virtual hand was my hand
Q2	It seemed as if I had more than one left hand
Q3	It seemed as if I were feeling a table in the location where the virtual hand was
Q4	It felt as if I no longer had a left hand, as if my left hand had disappeared
Q5	Was visual feedback synchronized to the tactile stimuli? [Tactile]/was cardio feedback in time with your own heartbeats? [Cardio]

from memorizing previous positions which could otherwise induce carry-over effects between tests (Tsakiris et al., 2011). For each trial, we computed as an objective measure of virtual hand ownership the "proprioceptive drift difference" PDD, which is the difference between pre-induction and post-induction PD, so that positive values indicated increased drift and hence increased ownership (Tsakiris et al., 2011).

2.6. Questionnaire

In the *questionnaire* period at the end of each trial, participants were presented with five questions sequentially via the HMD (see Table 1; the rest of the image was black). The order of presentation was the same in each trial. Participants answered each question using the input device. The first four questions were adapted from Botvinick and Cohen (1998), [Q1–Q4] and were designed to assess the strength of the subjective experience of virtual hand ownership. Question 5 asked participants to judge whether cardio-visual or tactile-visual feedback had been synchronous or asynchronous.

2.7. Interoceptive sensitivity

Individual IS was measured by a "feedback" task based on Whitehead, Drescher, Heiman, and Blackwell (1977), in which participants were asked to judge whether auditory cardiac feedback was synchronous or asynchronous with their heartbeat. Auditory feedback was provided as 150 ms pulses of a 2000 Hz tone, which in the synchronous condition, were timed to occur 230 ms after the electrocardiographic R-wave signifying diastole (estimated to occur 120 ms prior to oximeter onset); asynchronous feedback was generated by altering the estimated heart-rate to be either faster (130%) or slower (70%) than that recorded by the oximeter. Participants completed 16 trials each lasting 10 s, 8 with synchronous and 8 with asynchronous (50% faster, 50% slower) feedback. IS was calculated as the proportion of correct trials. We chose this method as opposed to an alternative based on counting heartbeats (Schandry, 1981) because it depends on comparing interoceptive and exteroceptive (auditory) signals and plausibly involves multisensory integration.

3. Results

3.1. Cardio-visual and tactile-visual feedback modulate proprioceptive drift

To examine whether the timing of cardio-visual and tactile-visual feedback modulated the experience of body ownership as measured by PDD, we performed a within-subject 2-way ANOVA with "condition" (cardiac still, cardiac move, tactile) and "feedback" (synchronous, asynchronous) as within-subjects variables. We found a main effect of both condition [$F(2,40)=5.00$, $p=0.012$] and feedback [$F(1,20)=17.81$, $p<0.001$]. Critically, we found a significant interaction between condition and feedback [$F(2,40)=47.97$, $p=0.019$)] indicating that the degree of modulation of PDD by feedback accuracy varied across conditions (Fig. 2). To explore this, we conducted planned *t*-tests comparing synchronous vs. asynchronous feedback in each condition, correcting for multiple comparisons using the false discovery rate (p_{FDR}, Benjamini & Hochberg, 1995). (Note that all *t*-tests reported in this paper were two-tailed.) PDD was significantly higher for synchronous as compared to asynchronous feedback in the conditions "cardiac still" [$t(20)=2.70$, $p=0.014$, $p_{FDR}=0.021$] and "tactile" [$t(20)=3.20$, $p=0.004$, $p_{FDR}=0.013$], but not in "cardiac move" [$t(20)=-0.34$, $p=0.714$]. Thus, according to the PDD measure, synchronous cardio-visual feedback leads to enhanced ownership (PDD= 3.16 cm, SEM ± 1.03) as compared to asynchronous feedback (PDD=1.02 cm, SEM ± 0.72). Note that there was no significant difference in PDD ("cardiac still" condition) between slow and fast asynchronous feedback [$t(40)=1.03$, $p=0.310$].

The same pattern of results held for synchronous (PDD=5.81 cm, SEM ± 1.03) as compared to asynchronous (PDD=1.81 cm, SEM ± 1.20) tactile-visual feedback, replicating the classical RHI findings. In the "cardiac move" condition PDD is high in both feedback conditions (synchronous PDD=4.51 cm, SEM ± 1.04; asynchronous PDD=4.51 cm, SEM ± 1.03) with no significant difference. PD magnitudes in our study (averaged across subjects) were comparable with those observed in other RHI experiments (Makin et al., 2008).

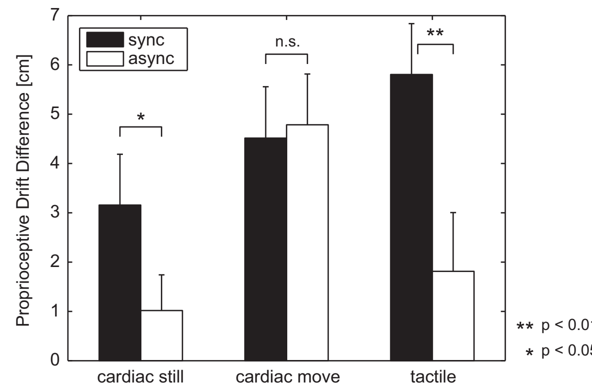

Fig. 2. Cardio-visual feedback modulates EBO as measured objectively by proprioceptive drift difference (PDD). PDDs were significantly larger for synchronous versus asynchronous cardio-visual feedback in the "cardiac still" but not the "cardiac move" condition. PDDs were also significantly larger for synchronous versus asynchronous tactile-visual feedback ("tactile" condition). Each bar shows the average across all participants along with standard errors.

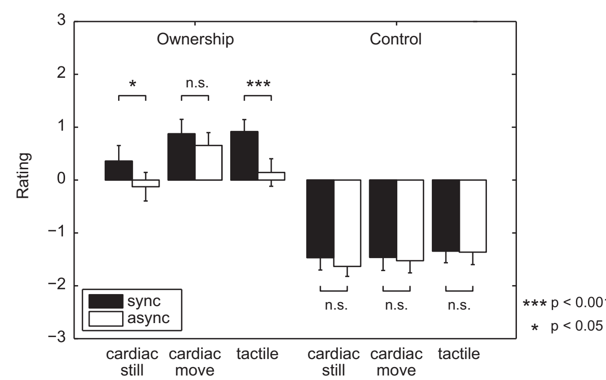

Fig. 3. Cardio-visual feedback modulates EBO as measured subjectively via questionnaire. Each bar shows mean (and standard error) visual analog scale responses for "ownership" questions and "control" questions. Ownership was significantly higher for synchronous feedback in both "cardiac still" and "tactile" conditions, but not in "cardiac move". There were no significant differences for the control questions in any condition.

3.2. Cardio-visual and tactile-visual feedback modulate subjective experience of ownership

We next analyzed data from the questionnaire presented on each trial by defining two variables: "ownership" as the average of ratings of questions 1 and 3, and "control" as the average across questions 2 and 4. Fig. 3 shows these summary statistics, averaged across subjects, in each condition (see Table S1 in *Supplementary information* for a full breakdown of responses). A within-subjects 3×2 ANOVA for "ownership" revealed significant main effects of both condition [$F(2,40)=6.8964$, $p=0.003$], and feedback [$F(1,20)=7.6237$, $p<0.001$], and an interaction approaching significance between condition and feedback [$F(2,40)=3.1802$, $p=0.052$], which we explored using planned *t*-tests comparing synchronous and asynchronous feedback. Consistent with the PD analysis, in condition "cardiac still" ownership was rated higher for synchronous (0.358, SEM ± 0.30) as opposed to asynchronous cardio-visual feedback (−0.126, SEM ± 0.27, $t(20)=2.366$, $p=0.028$, $p_{FDR}=0.042$) (units reflect a continuous visual-analog scale with range [−3,3]). The same pattern was found in the "tactile" condition (synchronous 0.916, SEM ± 0.23; asynchronous 0.143, SEM ± 0.23; $t(20)=4.409$,

$p<0.001$, $p_{FDR}<0.001$), but fell just short of significance in the "cardiac move" condition where ownership was rated high for both synchronous (0.874, SEM $\pm$ 0.27) and asynchronous (0.655, SEM $\pm$ 0.27) cardio-visual feedback [$t(20)=1.884$, $p=0.074$, $p_{FDR}=0.074$]. Importantly, there were no significant main effects nor any interaction in a second within-subject 2-way ANOVA using the "control" ratings as the dependent variable [for condition ($F(2,40)=1.482$, $p=0.241$), for feedback ($F(1,20)=1.191$, $p=0.288$), for the interaction ($F(2,40)=0.259$, $p=0.773$)]. Planned t-tests comparing synchronous and asynchronous feedback were non-significant ($p_{FDR}>0.5$ in all control conditions). Visual-analog ratings for the control questions were all substantially lower than for the ownership questions (Fig. 3) underlining that modulation of subjective experience in this paradigm was specific to ownership. Together, these findings confirm that synchronous but not asynchronous cardio-visual feedback enhances the experience of ownership of the virtual hand.

One might worry that data from subjective questionnaires might not be normally distributed, potentially undermining inferences drawn using parametric ANOVA analysis. To reassure on this point we note (i) our subjective data consisted of continuous responses (not discrete Likert scale responses) and involved summing two separate responses for each variable, thus facilitating normality, and (ii) ANOVAs are in any case widely considered robust to deviations from normality (Lix, Keselman, & Keselman, 1996). Nonetheless we explicitly tested for normality of the "ownership" and "control" variables in each condition using the Lilliefors test. After correcting for multiple comparisons all data sets passed this test. The full set of results from these tests is given in Table S2 in the *Supplementary information.*

3.3. Relation between awareness of cardio-visual feedback accuracy and EBO

We next wondered whether the experience of ownership was influenced by the degree to which subjects were aware of feedback synchrony. Addressing this, Q5 in the questionnaire asked participants to judge whether the visual feedback was synchronous with their heartbeat (cardio-visual conditions) or with the tactile stimulation (tactile condition). A within-subject 2-way ANOVA with average responses to Q5 as the dependent variable showed a main effect of feedback ($F(1,20)=49.70$, $p<0.001$) but not condition ($F(2,40)=1.271$, $p>0.25$) with a significant interaction between condition and feedback ($F(2,40)=44.75$, $p<0.001$). Planned t-tests revealed that participants detected synchronous feedback more accurately in conditions "cardiac still" ($t(20)=3.020$, $p=0.007$, $p_{FDR}=0.010$) and "tactile" ($t(20)=10.92$, $p<0.0001$, $p_{FDR}<0.0001$) but not "cardiac move" ($t(20)=0.416$, $p=0.682$); see Fig. 4A. While tactile-visual synchrony is obviously easy to notice for every participant (indeed it is rarely tested in the classical RHI), the finding that cardio-visual synchrony could also be detected (in the absence of distracting hand movements) raised the possibility that the modulation of experience of ownership in this condition may be mediated by awareness of this relation. To explore this, we used a median split to divide participants into two groups, based on their responses to Q5, to form "high" and "low" awareness groups. The high awareness group was defined by correctly answering Q5 at or greater than the median rate ($=0.75$) in the "cardiac still" condition ($n=13$), while the low awareness group comprised those participants who correctly answered Q5 at less than the median rate ($n=8$). Fig. 4B shows PDD scores for these two

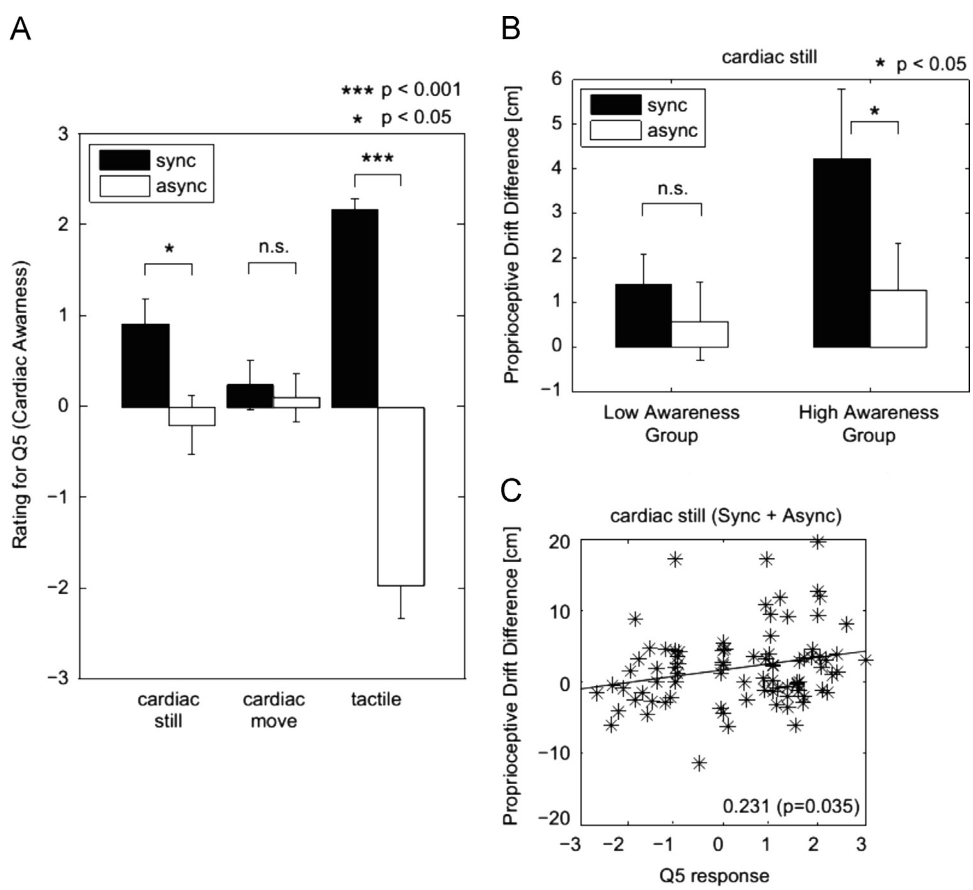

Fig. 4. Influence of cardio-visual feedback depends on awareness of synchrony. (A) Average visual analog responses to Q5 which asks participants to judge feedback synchrony. (B) PDDs for synchronous and asynchronous cardio-visual feedback (condition "cardiac still" only) grouped into "low" and "high" awareness groups defined by accuracy of responses to Q5 (top panel); the same data are replotted as a scatter plot below. (C) Correlation between PDD and response to Q5 for all participants in condition "cardiac still"; each point represents a single trial. There is a significant positive correlation.

groups for both asynchronous and synchronous cardio-visual feedback. A between-subject 2×2 ANOVA with PDD as the dependent variable found no significant main effects for either feedback [synchronous vs. asynchronous ($F(1,38)=1.89$, $p=0.177$) or awareness ["low aware" vs. "high aware", ($F(1,38)=2.15$, $p=0.151$)], or their interaction ($F(1,41)=0.69$, $p=0.413$). However, planned two-sample t-tests comparing PDD values between cardio-visual feedback conditions revealed significantly greater PDD for synchronous than asynchronous feedback for the high awareness group only ("high", $t(12)=2.996$, $p=0.011$, $p_{FDR}=0.022$; "low", $t(7)=0.643$, $p=0.54$). We note that this result should be interpreted with caution given the lack of a significant interaction in the higher-order ANOVA.

To further examine this issue we computed the correlation between PDD and responses to Q5, for all participants, in the "cardiac still" condition. As shown in Fig. 4C there is a significant positive correlation (Spearman's rank$=0.231$, $p=0.035$). A similar result holds for the correlation between Q5 responses and subjective ownership scores (Spearman's rank$=0.297$, $p=0.006$). Taken together, these analyses indicate that awareness of cardiac synchrony may play an important role for experiences of ownership when synchronous cardiac feedback is given.

3.4. Influence of cardio-visual feedback is associated with interoceptive sensitivity

How do our results depend on individual interoceptive sensitivity (IS)? Fig. 5 shows correlations between PDD values (shown as the difference between synchronous and asynchronous feedback) and IS for both "cardiac still" and "tactile" conditions. (We do not analyze "cardiac move" because of the lack of difference in PDD between feedback conditions.) One outlier (based on three standard deviations from the mean) was removed from the "tactile" condition. There was a significant positive correlation between IS and PDD in the "tactile" condition (Spearman's rank correlation coefficient 0.509, $p=0.022$, $p_{FDR}=0.044$), and a non-significant correlation in the "cardiac still" condition (correlation$=0.207$, $p=0.368$). We further analyzed this data by dividing participants into high IS ($n=8$) and low IS ($n=13$) groups using a median ($=0.750$) split. Fig. 5B shows PDDs for each group in both feedback conditions and for "tactile" and "cardiac still" conditions. In the "tactile" condition, a 2-way ANOVA with "feedback" and "IS group" as variables showed a significant main effect of feedback ($F(1,36)=4.98$, $p=0.03$), but not for IS group ($F(1,36)=0.23$, $p=0.64$), nor for the interaction ($F(1,39)=1.61$, $p=0.21$). However, planned t-tests comparing synchronous versus asynchronous feedback showed a significant difference in PDD in the high IS group ($t(14)=3.06$ $p<0.01$, $p_{FDR}=0.017$), but not the low IS group ($t(22)=0.67$, $p=0.51$) reflecting significant modulation of PDD by tactile-visual feedback for high IS participants only (high IS, sync$=6.09$ cm, SEM $\pm$ 1.18, async$=0.84$ cm, SEM $\pm$ 1.24; low IS, sync$=4.91$ cm, SEM $\pm$ 1.47; async$=3.46$ cm, SEM $\pm$ 1.57). In the "cardiac still" condition a 2-way ANOVA showed marginal main effects of feedback ($F(1,38)=3.49$, $p=0.07$) and IS group ($F(1,38)=3.10$, $p=0.09$), with no significant interaction ($F(1,41)=0.10$, $p=0.75$). In this condition, while PDD was generally higher for synchronous cardio-visual feedback (compatible with Fig. 2), this difference did not significantly differ between IS groups.

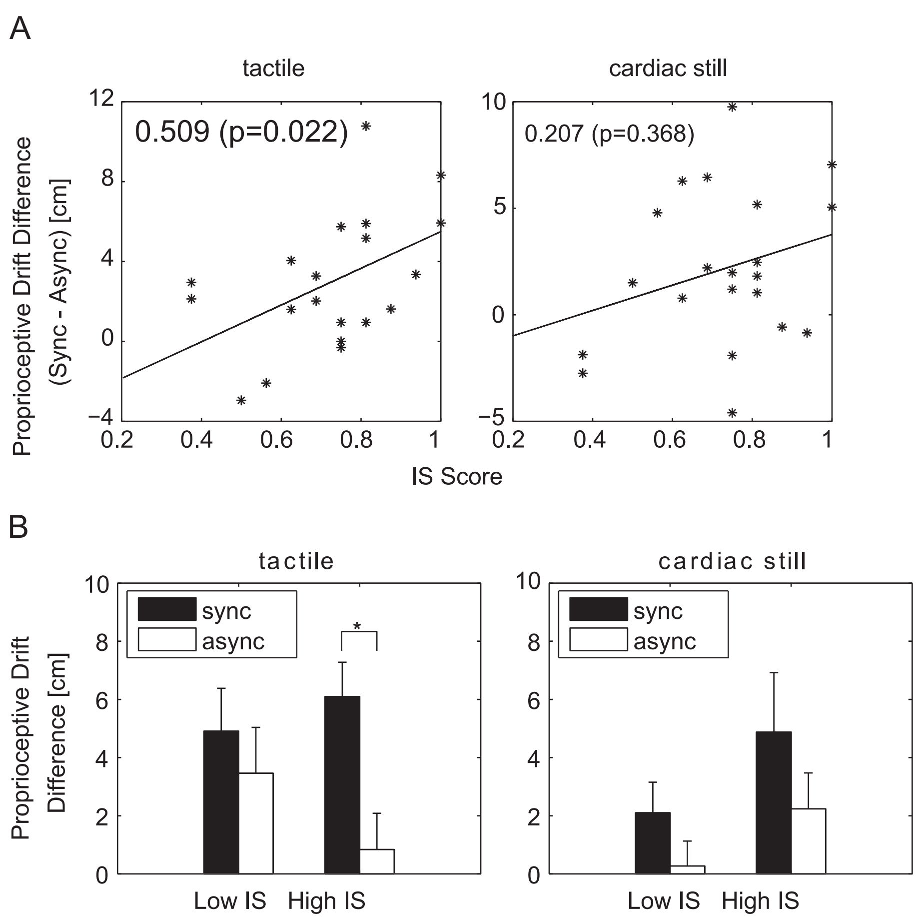

Fig. 5. Individual interoceptive sensitivity modulates the influence of feedback on the experience of ownership. (A) Correlation between individual IS and PDD (synchronous minus asynchronous feedback) for both "tactile" and "cardiac still" conditions. (B) The same data grouped by a median split into low and high IS groups, showing PDD for synchronous and asynchronous feedback separately.

Planned t-tests between the feedback conditions did not show any significant differences. Analysis of subjective responses showed a similar pattern. IS showed a marginal correlation with mean visual-analog responses to ownership questions in the "tactile" (Spearman's rank=0.427, $p=0.053$, $p_{FDR}=0.106$) but no correlation in the "cardiac still" condition (correlation=0.02, $p=0.930$). Because these correlations were at best marginal we did not conduct a median split analyses on these data.

4. Discussion

We sought to determine whether multisensory integration across exteroceptive and interoceptive domains influences the experience of body ownership (EBO) in a version of the rubber-hand illusion. We combined augmented reality (AR) and simultaneous physiological monitoring to implement a "virtual rubber hand" on which we projected cardio-visual feedback so that the visual appearance of the virtual hand was modulated by cardiac signals, either in-time or out-of-time with each participant's heartbeat. We further examined the role of proprioceptive-visual integration induced by finger movements, and we related our observations to individual differences in interoceptive sensitivity (IS). The findings establish directly that multisensory integration of exteroceptive and interoceptive signals can modulate EBO in the rubber hand illusion. Specifically, we found that synchronous (as compared to asynchronous) cardio-visual feedback led to an enhanced experience of ownership of the virtual hand (condition "cardiac still"), as measured objectively by proprioceptive drift (Fig. 2), and subjectively by questionnaire (Fig. 3). This observation extends previous studies showing correlations between IS and susceptibility to illusions of body ownership (Tsakiris et al., 2011) and associations between specific physiological measures and RHI induction (Barnsley et al., 2011; Moseley et al., 2008). Our findings, in relating to an accessible (and much studied) illusion, also extend recent complementary observations of facilitation of proprioceptive drift when cardiac signals are incorporated within a virtual reality avatar in a generalized full-body illusion (Aspell et al., in press).

The results also replicate the classic RHI (condition "tactile") by showing that synchronous as compared to asynchronous tactile-visual feedback enhanced EBO, again as measured both objectively and subjectively. Condition "cardiac move" elicited strong EBO as measured by both methods. This condition tested effects during both (synchronous or asynchronous) types of cardio-visual feedback with congruent (always synchronous) visual remapping of intentional finger movements onto the virtual hand. Interestingly, neither objective nor subjective measures differed as a function of cardio-visual feedback, indicating that in this condition the integration of proprioceptive and visual signals induced by the finger movements dominated the influence of interoceptive feedback on EBO.

We found suggestive evidence that the strength of EBO (in the condition "cardiac still") depended on the degree to which participants were able consciously to discriminate synchronous from asynchronous cardio-visual feedback (Fig. 4). This suggests that multisensory integration across interoceptive and exteroceptive domains modulates EBO preferentially via consciously accessible representations of interoceptive state. This result might suggest a positive correlation should exist between individual IS and strength of the illusion. However, while we observed a trend in this direction it did not reach significance (Fig. 5). We note the role of conscious mediation is usually taken for granted in the classical RHI, in which it is trivially easy for participants to distinguish synchronous from asynchronous tactile-visual feedback (as we confirm explicitly, Fig. 4A).

While the correlation between IS and PDD did not reach threshold significance in the "cardiac still" condition, we did observe a significant positive correlation between IS and PDD in the "tactile" condition (Fig. 5). At first glance this result appears to conflict with data reported by Tsakiris et al. (2011) which show a significant negative correlation between IS and PDD in the classical RHI. These latter results have been interpreted by the idea that low IS could mean that a participant is less "in touch" with his/her own body and therefore more susceptible to manipulations of EBO by exteroceptive cues (Apps & Tsakiris, 2013; Tsakiris et al., 2011). What could account for the opposite pattern of results in our data? One possibility is that Tsakiris et al. used a different method for assessing IS based on asking subjects to count the number of heartbeats in time-periods of varying lengths (Schandry, 1981). Indeed when we repeated our IS measures using this task, there was no significant positive trend between IS and PDD (see *Supplementary information*). There were also differences in the number of subjects in our study ($n=21$) and in the Tsakiris et al. study ($n=46$), as well as differences in mean IS across participants (0.77 vs. 0.64). These differences could account for the discrepant results at least in part, especially when recalling that our choice of IS method (Whitehead et al., 1977) was motivated by its reliance on comparing interoceptive and exteroceptive (auditory) signals: this method may be more likely to be modulated by processes underlying multisensory integration than the alternative "counting" method (Schandry, 1981).

A second possible explanation turns on the observation that the classical RHI fake hand (as used by Tsakiris et al., 2011) is usually very distinct visually from the appearance of a participant's real hand, whereas the virtual hand in our paradigm is a high-fidelity three-dimensional visual copy of each participant's real hand. Thus, if high IS individuals place a higher weighting on interoceptive signals (Tsakiris et al., 2011), this could lead to a higher *a priori* willingness to accept the virtual hand in our paradigm, as compared to the classical RHI where the *a priori* plausibility of a rubber hand being part of the body is relatively low. This difference in *a priori* plausibility could account for the opposite relationships between IS and PDD in the two paradigms, since synchronous tactile-visual feedback would be incongruent with the prior in the classical RHI, and congruent with the prior in our study. Taking this idea further it could be argued that our paradigm assesses the extent to which participants feel embodied in their own body (albeit with conflicting proprioceptive signals), as compared to the classical RHI which assesses susceptibility to incorporation of foreign bodies or body parts within the body image. Further research is warranted discriminate these possible explanations and to explore systematically how individual differences in IS correlate with susceptibility to manipulations of EBO across paradigms.

The RHI has been explained with reference to models of multisensory integration which propose that conflicts between vision, touch, and proprioception are minimized by visual capture of visual and felt (tactile) events occurring in close peri-hand space, on the basis of statistical correlations among sensory signals together with visual dominance (Botvinick & Cohen, 1998; Makin et al., 2008). This process is argued to update self-representations to incorporate the fake hand. However, updating of self-representations is evidently constrained by prior "beliefs" on the reliability of sensory input (e.g., vision dominates proprioception in the classical RHI) and on the plausibility of an object being part of the body. The latter point is amply demonstrated by abolition of the RHI for non-hand-like objects (Tsakiris, Carpenter, James, & Fotopoulou, 2010), and by implausibly oriented or positioned fake hands (Ehrsson, Spence, & Passingham, 2004; Lloyd, 2007; Tsakiris & Haggard, 2005). The importance of peri-hand space can also be considered as a prior, in the sense that sensory signals inferred to closely aligned spatial locations are more likely to be interpreted as arising from a common source. These observations are consistent with an emerging theoretical view of selfhood based on *predictive coding* which extends multisensory integration accounts (Apps & Tsakiris, 2013; Seth et al., 2011) and which also well accounts for both the interoceptive and proprioceptive effects in the present results. Essentially, the predictive coding view adapts to the case of self-perception the “Bayesian brain” framework, which describes perception as the process of inference about the most likely causes of sensory input (Clark, 2013; Friston, 2009). On this view, self-representations consist in multi-level (hierarchical) generative (i.e., predictive) models of the causes of those sensory signals which are deemed most likely to be “me” (Apps & Tsakiris, 2013). In Bayesian terms, this is the posterior probability of the most likely generative model (self-representation) given a set of priors and current sensory input. Crucially, minimization of prediction errors – such as those induced by multisensory conflicts during the RHI – will update the posterior probabilities and, over time, can induce changes in priors (perceptual learning). In addition, priors reflecting high-level representations such as “self” and body-ownership are likely to operate at relatively abstract multisensory levels. Thus, statistical correlations among highly weighted sensory signals (vision, touch) can overcome prediction errors in a different modality (proprioception) leading to a revised multisensory generative (predictive) model which minimizes the overall level of self-related prediction error by incorporating the fake hand as part of the self-representation.

Our results fit nicely into such a predictive framework when it is extended to incorporate interoceptive signals. “Interoceptive predictive coding” (Seth et al., 2011; Critchley & Seth, 2012) is essentially the idea that interoceptive self-representations – and emotional feeling states – arise from generative models of causes (both external and internal) of interoceptive afferents. In relation to the RHI this means that interoceptive signals constitute just one more sensory modality to be incorporated into multisensory predictive models of the body and self. Thus, statistical correlations between interoceptive (e.g., cardiac) and exteroceptive (e.g., visual) signals can lead to updating of predictive models of self-signals through minimization of prediction error, just as may happen for exteroceptive multisensory conflicts in the classic RHI. In other words, there is no need to assume distinct modes of influence of exteroceptive and interoceptive signals on EBO, for example that the former is based on multisensory integration and the latter on trait-based modulation of this integration (Tsakiris et al., 2011). In addition, if it is further assumed that predictive models are continually probed by control signals which attempt to confirm the currently dominant model [“active inference”, Friston et al., 2010], the framework naturally accommodates the phasic physiological changes accompanying RHI induction (Barnsley et al., 2011; Moseley et al., 2008) when these changes are taken to reflect altered autonomic control. Other recent results correlating individual IS with susceptibility to changes in self-representation under multisensory stimulation have also been interpreted within this emerging framework (Tajadura-Jimenez & Tsakiris, in press).

A framework of predictive multisensory integration across interoception and exteroception is further supported by anatomical and neuroimaging evidence. The right-hemisphere anterior insular cortex provides one cortical focus for the integration of exteroceptive and interoceptive signals (Craig, 2009; Critchley & Harrison, 2013; Critchley et al., 2004; Seth et al., 2011). This region has been proposed as a neural substrate for self-awareness in the form of the “material me” (Craig, 2009), and is activated by mismatches between predicted and actual interoceptive signals induced by false physiological feedback (Gray, Harrison, Wiens, & Critchley, 2007). In addition, anterior insular activity elicited during intentional action is associated with interoceptive evaluations of the affective consequences of motor intentions (Brass & Haggard, 2010). Activity within the nearby mid-posterior insula correlates with EBO during the classical RHI (Tsakiris, Hesse, Boy, Haggard, & Fink, 2007), and damage to this area is associated with delusions of body ownership including denial of paralysis and somatoparaphrenia (Vallar & Ronchi, 2008). Thus the right insular lobe could form a central hub within a functional network instantiating predictive models of body ownership and self.

The strong experience of ownership during the “cardiac move” condition for both synchronous and asynchronous cardio-visual feedback also makes sense in light of a predictive coding account. In this condition, while there remains a conflict in global (relative to the body) proprioceptive signals, the visual remapping of finger movements to the virtual hand induces strong correlations between visual signals and local (hand-related) proprioceptive input. This is another example of active inference increasing the likelihood of incorporating the virtual hand into the body image, as compared to the “cardiac still” condition where no such movement-based active inference takes place. Thus, in the “cardiac move” condition the visual and proprioceptive signals are given sufficiently high weighting to suppress the influence of interoceptive prediction error on the most likely predictive model. By the same token, when real-hand movements are not reflected in the fake hand, as in the classical RHI, one would expect the illusion to be abolished, as indeed it is (Banissy & Ward, 2013; Tsakiris, Longo, & Haggard, 2010). In addition, as suggested earlier, the close visual similarity of the virtual hand in our paradigm – as compared to the classical RHI – may induce a stronger prior that the virtual hand is part of the body, such that increased IS could lead to increased susceptibility to the RHI, as shown in our data (Fig. 5), and in contrast to results found using the classical RHI (Tsakiris et al., 2011).

The “cardiac move” condition also highlights important connections between experiences of agency (i.e., the experience of being the author of an action) and ownership (David, Newen, & Vogeley, 2008; Tsakiris et al., 2010). The real-time visual remapping of finger movements in this condition does induce an experience of agency, as compared to the other conditions, though this is not an effect we measured formally in this study. Future research will adapt our paradigm to assess systematically the relative contributions of motor corollary discharge and both proprioceptive and visual prediction errors in determining experiences of both ownership and agency. We speculate that experienced agency will depend on highly weighted proprioceptive prediction errors which are accounted for by a stack of hierarchical predictions which include at higher levels those related to intentions and goals.

In summary, our data show that multisensory integration of interoceptive and exteroceptive signals can influence EBO in a manner that is well accounted for by predictive models of multisensory integration among self-related signals. The results underscore the potential for combined AR and physiological monitoring within experiments investigating how various aspects of selfhood depend on predictive models of selfhood integrating interoceptive and exteroceptive domains.

Acknowledgments

This study was supported by ERC project CEEDS (FP7-ICT-2009-5; 258749) with additional support from the Dr. Mortimer and Theresa Sackler Foundation and EPSRC Fellowship G/700543/1 to AKS. We are grateful to other members of the CEEDs consortium for helpful in discussions (in particular Paul Verschure) and to Alessandro Pappagallo for help with data collection.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2013.08.014.

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